A restudy of Rhinocerotini fossils from the Miocene Jiulongkou Fauna of China

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Abstract   All the extant rhino species belong to Rhinocerotini and either have one horn (a nasal horn) or two horns (a nasal horn and frontal horn). So far, the earliest Rhinocerotini to have been identified in China is the "*Dicerorhinus*" *cixianensis*, which was based on a juvenile skull with an associated mandible from the Middle Miocene locality of Jiulongkou in Cixian County, Hebei Province of northern China. Our analyses suggest that there are similarities between this specimen and the modern genus, *Dicerorhinus*, but it differs in several cranial traits and therefore cannot be assigned to the modern genus. Instead, it is closer to the Middle Miocene *Lartetotherium* from Europe, especially the specimen from La Retama in Spain and should be assigned to that genus, indicating the presence of intracontinental dispersal at this time. The Jiulongkou fauna is the only Middle Miocene fauna with Rhinocerotini in China, and, together with the faunal composition, this implies a more humid and closed environment, in contrast to those found in western China. We suggest that the position of the posterior border of the nasal notch is a good indication of the specimen's evolutionary level in Rhinocerotini. The anterior position of the nasal notch as seen in modern *Dicerorhinus*, together with its certain similarities to *L. cixianensis* as well as its differences with more specialized species of the *Dihoplus-Pliorhinus-Stephanorhinus-Coelodonta* lineage, supports the conclusion that *Dicerorhinus* experienced little change during a nearly 10 Myr evolutionary history, possibly due to the low selection pressure seen in the tropical/subtropical forests in southeastern Asia.

Key words   Jiulongkou, Middle Miocene, *Lartetotherium cixianensis*, Rhinocerotini

1   Introduction

All modern rhinos have either one or two horns on their noses and frontals. The Rhinocerotini tribe probably originated in Africa, with the earliest known species, *Rusingaceros leakeyi*, discovered in Rusinga, eastern Africa (Hooijer, 1966; Werdelin and

Sanders, 2010). *Rusingaceros leakeyi* was found in the Wayando Formation (Rusinga) of Kenya, with an age of 18 Ma, early Kisingirian (Van Couvering and Delson, 2020), and it is equivalent to MN3 in Europe (Mein, 1999). So far, the earliest record of Rhinocerotini in Eurasia comes from Bezian, La Romieu, France, MN4b, represented by several isolated teeth assigned to *Lartetotherium sansaniense* (Ginsburg and Bulot, 1984). *Lartetotherium sansaniense* was the most common Rhinocerotini in the Middle Miocene of Europe. This species was first discovered in the classical MN6 locality Sansan, France, and identified as *Rhinoceros sansaniense* (Lartet, 1851), and was erected to a separate genus *Lartetotherium* by Ginsburg (1974). It is found over the period of MN4-MN9 in Europe, which is a rather long time span, but as Heissig (1999) commented on: the poor preservation of most of the materials masks the differences between the species. Another Middle Miocene Rhinocerotini species is *Gaindatherium browni*, which was discovered in Chinji Rest House, Salt Range, Attock District, Punjab (Colbert, 1934, 1935). Both *L. sansaniense* and *G. browni* are well-known, and they are included in recent phylogenetic analyses (Pandolfi et al., 2021; Antoine et al., 2022).

In contrast to these well-known species, the early Rhinocerotini record in eastern Asian is very poor. So far, the only record of the species is from Jiulongkou in Cixian County, Hebei Province of North China (Chen and Wu, 1976). This fauna has abundant fossil remains and can be viewed as the early Tunggurian, which is equivalent to MN6 of Europe (Deng, 2006). The partial cranium and mandible of a juvenile individual were used to erect a new species *Dicerorhinus cixianensis* by Chen and Wu (1976). Some postcranial bones from this locality were assigned to *Dicerorhinus* sp., and a premaxilla fragment was assigned to the Rhinocerotidae gen. et sp. indet. (Chen and Wu, 1976). This species has received little attention from most researchers (Qiu, 1990; Tong, 2012). Considering that it is the only pre-Late Miocene Rhinocerotini discovered in East Asia, it has potential importance for helping to increase our understanding of the early evolution of Rhinocerotini, which flourished since the Late Miocene. The specimens of *D. cixianensis* are redescribed and analyzed in this study.

2   Materials and methods

The materials (include a juvenile skull with mandible IVPP V4833, and a premaxilla IVPP V4841) described in this study are housed in the IVPP. For cranial measurements and anatomical terms, we follow those of (Deng, 2004; Antoine and Saraç, 2005; Qiu and Wang, 2007). Measurements were made either with caliper (dentition) or in the 3D models (crania and mandibles). Measurements are seen in Table 1.

Abbreviations   AMNH, American Museum of Natural History, New York, USA; HMV, Hezheng Paleozoological Museum, Hezheng, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMNH, Muséum national d'Histoire naturelle, Paris, France; AW, anterior width of the cheek teeth; L, length; M/m, upper/lower molar; P/p, upper/lower premolar; PW, posterior width of the cheek teeth; W, width.

3   Systematic paleontology

Order Perissodactyla Owen, 1848
Superfamily Rhinocerotoidea Gray, 1821
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae (Gray, 1821)
Tribe Rhinocerotini Gray, 1821
Genus *Lartetotherium* Ginsburg, 1974
***Lartetotherium cixianensis* (Chen and Wu, 1976)**

Dicerorhinus cixianensis Chen and Wu, 1976, p. 8

Dicerorhinus cixianensis Qiu, 1990, p. 540

Dicerorhinus cixianensis Cerdeño, 1996a, p. 29

Dicerorhinus cixianensis Tong, 2012, p. 557

Dicerorhinus cixianensis Deng, 2015, p. 133

Dicerorhinus cixianensis Pandolfi, 2018, p. 28

Holotype   Partial cranium and associated mandible of a juvenile individual (IVPP V4833).

Type locality and horizon   Jiulongkou, Cixian County, Hebei Province; Middle Miocene, early Tunggurian, equivalent to MN 6 of Europe (Deng, 2006).

Description   The type skull IVPP V4833 represents a juvenile individual. The DP1–4 are present, M1 half erupts, and the tip of the M2 cusp is just breaking the alveolus.

The skull seems to be dolichocephalic (Fig. 1B). It is relatively low. The dorsal profile of the skull in the preserved part is mostly straight, only the anterior part of the nasal is turning
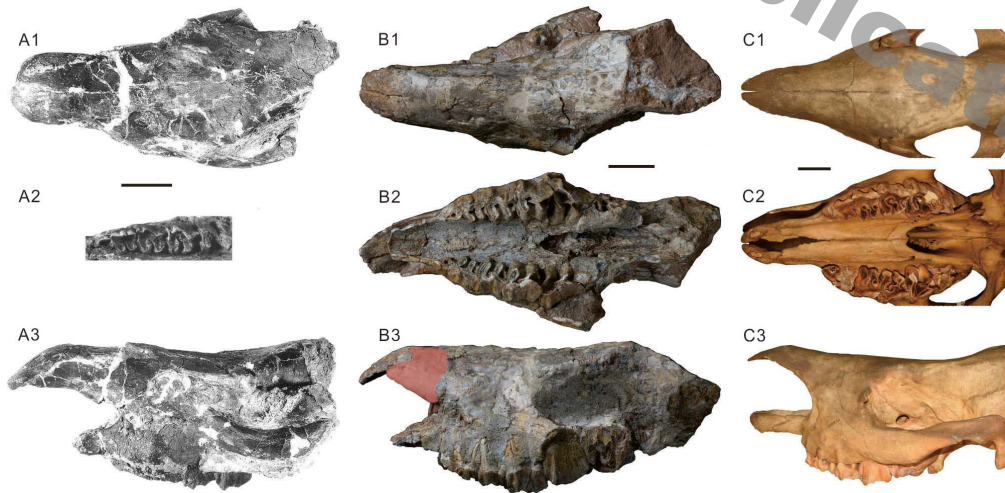

Fig. 1   Comparison of craniums in dorsal (A1, B1, C1), ventral (A2, B2, C2), and lateral (A3, B3, C3) views
A. *Lartetotherium* cf. *L. sansaniense* CSIC RE927, La Retama, Spain (Cerdeño, 1996a) (A3 reversed);
B. *L. cixianensis* IVPP V4833 (plaster at nose is marked in red) Jiulongkou, Hebei, northern China;
C. *Dicerorhinus sumatrensis* AMNH M173576. Scale bars=5 cm

downward. The nasal septum is not ossified, and the nasal bone is not wide, with a slightly domed horn base. The nasal notch reaches the level of the anterior border of the DP1. The nasal notch is V-shaped. The area has an indistinct rough vascular print on the surface of the nasal. The anterior part of nasal bones is not fully fused and has a distinct median groove that extends from the tip of the nasals to the top of the horn dome.

The infraorbital foramen is open at the level of the DP2. The anterior border of the orbit is above the posterior part of the DP4. Both the lacrimal process and preorbital process are absent. The postorbital processes of the frontal are weak and indistinct. The forehead has a smooth surface without any vascular print.

The premaxilla is thin and rather elongated (Fig. 2A). A premaxillae notch is still not present in the preserved part, which suggests the existence of a shallow notch in this species. There is also no indication of an incisor alveolus in the preserved part. The cheek toothrows on both sides diverge backward. The anterior border of the bony choana reaches the level of the DP4.

Fig. 2   Comparison of premaxillae in ventral view
A. *Lartetotherium cixianensis* IVPP V4841 Jiulongkou, Hebei, northern China;
B. *Dicerorhinus sumatrensis* V2877, Liucheng *Gigantopithecus* Cave, Guangxi, southern China;
C. *D. sumatrensis* MNHN A7965

The mandible is from the same individual with skull (Fig. 3). The left side is largely complete, whereas the right side lacks the ascending ramus. The horizontal ramus is shallow. Its anterior part is markedly shallower than the main body, and the ventral profile of the mandible is convex. The symphysis is narrow and long. The posterior border of the symphysis reaches the level of the p3. The mental foramen is present below the dp1. The ascending ramus is not relatively massive. Its anterior border is posteriorly inclined. The mandibular condyle is slightly transversely convex. The coronoid process is small, with a hook-like posterior border.

There is a single large incisor alveolus for the I1 in the premaxilla of IVPP V4841 that we tentatively assigned to the same species as the skull. The alveolus is elongated and has an oval shape. There is no alveolus for the I2. There is a distinct lateral groove in the maxilla. The premaxilla notch in the central is shallow.

Fig. 3   photographs of the mandible of *Lartetotherium cixianensis* IVPP V4833, Jiulongkou, Hebei, northern China
A. anterior view, showing the di1; B, C, E. medial (B), ventral (C) and lateral (E) views of the left side; D. lateral view of the right side

The upper deciduous teeth (Fig. 1B2) are low crowned, the lingual and labial cingulum absent, and the anterior and posterior cingula are developed. The outline of the DP1 is roughly triangular and wider in the back. In the DP1, the paracone fold is weak, the protocone and hypocone are conjoined on the lingual side, the protoloph is present and the protocone is small, the hypocone connects to the metacone, and the postfossette is closed. There is a weak crest between the protocone and the front end of the ectoloph, forming a closed shallow valley in the left DP1. The DP2 has an apparent mesostyle, the crochet and crista are weak and speared, and the protoloph and metaloph are simple and incline backwards. The DP3 is similar to the DP2, except that the DP3 has a metacone fold instead of a mesostyle. In the DP4 and M1, the crochet is well developed and simple, and the paracone has a weak constriction. The M2 is not entirely erupted, and a well-developed crochet like that in the M1 can be seen.

Table 1 Measurements of *Lartetotherium cixianensis*, Jiulongkou		(mm)
Measurement	Left	Right
Distance between nasal tip and bottom of nasal notch	62.73	75.08
Distance between nasal notch and orbit	110.16	121.66
Width of nasal base	70.71	
Cranial height in front of M1	136.91	142.27
Width of palate in front of M1	120.06	
DP1–4 L	118.82	119.03
I1 L (alveolus)	35.13	33.24
I1 W (alveolus)	17.82	17.94
DP1 L	19.72	21.46
DP1 W	18.13	20.25
DP2 L	>29.15	27.57
DP2 W	30.17	30.35
DP3 L	35.62	37.38
DP3 W	36.99	38.27
DP4 L	43.02	41.44
DP4 W	42.21	40.89
M1 L	49.35	49.2
M1 W	49.41	45.91
Distance between posterior borders of symphysis and ascending ramus	217.92	
Height of horizontal ramus in front of dp2	59.75	
Height of horizontal ramus in front of dp3	61.13	
Height of horizontal ramus in front of dp4	64.61	
Height of horizontal ramus in front of m1	56.15	63.62
Width of symphysis	41.11	
Antero-posterior diameter of ascending ramus	98.85	
Transverse diameter of condyle	>44.24	
Height at condyle	>142.67	
Height at coronoid process	169.79	
dp1–4 L	114.57	109.74
di1 L	6.84	6.59
di1 W	6.68	6.43
dp1 L	20.82	14.69
dp1 W	11.03	9.28
dp2 L	20.49	21.89
dp2 W	15.52	14.4
dp3 L	35.03	34.88
dp3 AW	18.11	17.24
dp3 PW	22.67	19.71
dp4 L	35.6	35.75
dp4 AW	24.22	19.85
dp4 PW	27.51	22.7
m1 L	41.3	>39.59
m1 AW	21.78	22.96
m1PW	27.21	22.27

Note: I1 L and I1 W come from V4841, others from V4833.

The lower deciduous teeth (Fig. 3) are low crowned and lack a cingulum. The structure of the dp1 is simple, with a small protoconid close to the ectolophid. The dp2 is heavily worn and partly broken, and a developed paraconid can be seen. The paralophid of the dp3 is wide, and there probably is a shallow valley in front of the paralophid before being worn down as seen in *Pliorhinus ringstroemi* (from personal observation). The trigonid of the dp3 and dp4 is angular,

while it is an obtuse dihedron in the dp3 and a right dihedron in the dp4. The m1 is similar to dp4, and its trigonid and talonid are more rounded.

4   Comparison

"*Dicerorhinus*" *cixianensis* was identified as *Dicerorhinus* due to its similarity to *Pliorhinus ringstroemi* (=*Dicerorhinus ringstroemi*) and *Lartetotherium sansaniense* (= *D. sansaniensis*) (Chen and Wu, 1976). As *D. kirchbergersis*, *D. choukoutienensis*, *D. yunchuensis* were all moved out of *Dicerorhinus*, the scope of the definition of *Dicerorhinus* became more restricted, and it is no longer appropriate to place "*D*". *cixianensis* in *Dicerorhinus*. Compared with "*D.*" *cixianensis*, the juvenile (M2 just beginning to sprout) and adult specimens of *D. sumatrensis* all have a large palatine fissure that starts at the front of the DP1, and the two sides of the premaxillae are not fused (Tong and Guérin, 2009; Chen et al., 2021). The palatine fissure of the juvenile "*D.*" *cixianensis* V4833 is invisible, and the adult premaxilla in V4841 is not elongated as in the modern *D. sumatrensis*, in which it extends close to the level of the I1. The rostral end of the nasal bone in *D. sumatrensis* is narrower, and the paracon of the DP1 is separate from the ectoloph. The crochet and crista of the DP2 are better developed, and they were connected after they were worn down. The mandible is shorter and wider (Chen et al., 2021). These characters differ from the modern *Dicerorhinus*, and suggest that the rhino from Jiulongkou can not be assigned to the modern genus.

A juvenile skull (M1 sprout completely) identified as *Lartetotherium* cf. *L. sansaniense* from La Retama, Spain (Cerdeño, 1996a) is most similar to that of the rhino from Jiulongkou. The minor differences are that the nasal of *L.* cf. *L. sansaniense* is slightly longer, and the crochet of the DP4 is relatively weak. The nasal notch in *L.* cf. *L. sansaniense* from La Retama and "*D.*" *cixianensis* are located before the level of the DP1, but in the adult *L. sansaniense* it is above the DP1 to P3 (Heissig, 2012). The position of the posterior end of the nasal notch, according to our observations, is relatively stable during the ontogeny process in rhinos (Fig. 4, *D. sumatrensis*, *Pliorhinus ringstroemi*, and *Chilotherium wimani*). It is likely that the nasal

Fig. 4   Nasal notch
A. *Dicerorhinus sumatrensis* (M1 just erupted) AMNH M173576; B. *D. sumatrensis* MNHN A7965;
C. *Pliorhinus ringstroemi* (DP4 erupted) HMV2049; D. *P. ringstroemi* HMV1115;
E. *Chilotherium wimani* (DP4 just erupted) X1934; F. *C. wimani* X108. Not to scale

notch of *L.* cf. *L. sansaniense* from La Retama and "*D.*" *cixianensis* in adults would still be the same as it is in the juveniles and would be located in front of cheek teeth as seen in *D. sumatrensis*. Heissig (2012) observed that the nasal notch tends to be posteriorly extended during the evolutionary process within *L. sansaniense*. This shows that the states of the nasal notch seen in *L.* cf. *L. sansaniense* and *D. sumatrensis* represent the primitive state, and the two species represent the early branch of Rhinocerotini.

Rusingaceros leakeyi (Hooijer, 1966) found from Africa is the earliest Rhinocerotini ever found (Geraads, 2010). The crochet and crista of the DP2 become more developed and connected after being worn. The crochet of the DP3 is developed. The I1 is large, and the I2 is absent. The shape of the incisor alveolus is close to that of "*D.*" *cixianensis*. *Gaindatherium browni* has a large I1 and a small I2 (Colbert, 1934). *Dihoplus schleiermacheri* also has a small I2, and all the other known Rhinocerotini have no I2. There are two horns present in *Rusingaceros leakeyi*, but only one horn present in *Gaindatherium*.

In summary, the Rhinocerotini from Jiulongkou are different from *Dicerorhinus* and the other known fossil Rhinocerotini. The juvenile nature of the materials has so far prevented a well-established diagnosis, but when considering the overall similarity and close chronology, the specimen is at this time best assigned to *Lartetotherium*, as *L. cixianensis*.

5   Discussion

As we have previously mentioned, the Jiulongkou rhino is different from the modern genus *Dicerorhinus* in several aspects, but it is still comparably more similar to other Late Miocene to modern Rhinocerotini, which are more specialized. In fact, *Lartetotherium* cf. *L. sansaniense* from La Retama (MN5a), Spain (Cerdeño, 1996a), *L. cixianensis* (MN6), and *D. sumatrensis* are similar to each other during the juvenile stage, whereas the adult individuals seem less similar, suggesting that some more specific traits are acquired during the ontogeny. As *Lartetotherium* is regarded as an ancestor of the modern Rhinocerotini (Pandolfi, 2018, 2023; Pandolfi et al., 2021), then it would appear that the major evolutionary tendency is for the nasal to become short and narrower. *Lartetotherium cixianensis* is probably closely related to the ancestor stock of modern *Dicerorhinus* and more derived than Plio-Pleistocene Rhinocerotini. The recent genomic phylogenetic inference suggested that the divergence of *D. sumatrensis* and other Asiatic rhinos (i.e. *Rhinoceros*) occurred at ~15Ma (Margaryan et al., 2020; Liu et al., 2021). This age is close to that of *L. cixianensis*. The anterior position of the nasal notch and simplified cheek teeth of the modern *Dicerorhinus* is rather close to that of *L. cixianensis*, supporting the interpretation that this genus was very conservative during its evolutionary history. This phenomenon is likely to be correlated with a relatively stable environment in the tropical or subtropical regions in southern China and southeastern Asia during the late Cenozoic, through which many ancient lineages survived (e.g., *Ailuropoda*, *Mydaus* and *Prionodon*) (Pocock, 1939, 1941;Fjeldsa and Lovett, 1997; Hwang and Larivière,

2003, 2004). The stable climate and abundant food resources bring on little selective pressures, whereas in more temperate regions, the global temperature fall (Zachos et al., 2001; Westerhold et al., 2020) and northern Eurasia aridification (Zhang et al., 2013; Liu et al., 2016; Kaya et al., 2018) significantly changed the environment rhinos lived in, and the Rhinocerotini there (e.g., *Dihoplus*, *Pliorhinus*, *Stephanorhinus* and *Coelodonta*) gradually evolved to have a larger size and more complicated cheek teeth (Deng et al., 2011; Tong, 2012; Pandolfi et al., 2021; Giaourtsakis, 2022).

The rhino from Jiulongkou is very close to the rhino from La Retama, MN5a of Europe, suggesting a potential biogeographic connection between eastern Asia and Europe existed at this time. Such connection during the Middle Miocene between Eurasia was not strong, as it has been revealed that at this time the northern part of eastern Asia (represented by the Tunggur Fauna) formed a relatively separate biorealm from Europe and south-southeastern Asia (Jiangzuo et al., 2020). This is likely to be correlated with a more open environment in eastern Asia, as exemplified by more abundant percrocutids and *Gobicyon*, which are cursorial and scavengers and are more likely to adopt an open environment (Qiu et al., 1988; Jiangzuo et al., 2019; Xiong, 2022).

Jiulongkou is slightly different from the localities mentioned above. It is so far the only known Middle Miocene locality in China to have produced Rhinocerotini. In the Tunggur Formation, two rhinos *Acerorhinus zernowi* and *Hispanotherium tungurense* are recorded, belonging to Acearatheriinae and Elasmotheriini, respectively (Cerdeño, 1996b; Wang et al., 2003). In the Dingjiaergou Fauna, four rhinos are present: *Caementodon tongxinensis*, *Hispanotherium matritense*, *Plesiaceratherium* sp., and *Alicornops laogouensis*, which belong to Elasmotheriini (first two), Aceratheriini, and Teleoceratini, respectively (Wang et al., 2016). Two rhinos are recorded from the Hujialiang Formation at Laogou locality of the Linxia Basin, i.e., *Alicornops laogouense* and *Hispanotherium matritense*, which belong to Teleoceratini and Elasomtheriini, respectively (Deng, 2003, 2004). Therefore, the combinations of rhinos seen in these localities are similar, dominated by the Acearatheriinae and Elasmotheriini in the Rhinocerotinae. Jiulongkou is unique in having Rhinocerotini, which is common in the Middle Miocene deposits from Europe (Filhol, 1891; Cerdeño, 1996a; Heissig, 1999, 2012; Antoine et al., 2000; Pandolfi, 2018) and southern/southeastern Asia (Colbert, 1934; Heissig, 1972; Khan et al., 2014).

The Jiulongkou fauna is composed of abundant samples *Palaeomeryx*, and there are also *Chalicotherium* and crocodiles (Chen and Wu, 1976; Chen and Liu, 2013; Qiu et al., 2013), which supports the presence of trees. However, the occurrence of some open-environment species (e.g., bone-cracking hyaenid *Percrocuta* and high-crowned *Turcocerus*) suggest a mixture of open and closed paleoenvironments in the fauna. In contrast, in the Dingjiaergou Fauna of similar age but located in the more western part (Wang et al., 2016), there are diverse acerorhinine and elasomotherine, abundant *Gobicyon* (Jiangzuo et al., 2019), and percrocutids (Xiong, 2022), and very few remains of *Palaeomeryx*, which implies a more open and arid

environment, and there are no reported Rhinocerotini. In any case, the Jiulongkou fauna shows a more predominantly closed environment compared with the other Middle Miocene sites previously mentioned. This is likely determined by its geography, which is closer to the ocean and has a lower altitude, and it is likely to have been more humid than the interior of Asia. The early Rhinocerotini are generally low-crowned and are therefore more likely to adapt to a closed environment. The presence of Rhinocerotini supports the interpretation that the Jiulongkou fauna is likely to be near to the ecological boundary between the open dominant environment from western China and the close dominant environment from coastal eastern Asia and southeastern Asia.

6   Conclusion

Through the restudy of the earliest Rhinocerotini of China and new comparative anatomical analyses, we suggest that Rhinocerotini from the Jiulongkou fauna should be excluded from the modern genus *Dicerorhinus*, and herein is assigned as *Lartetotherium cixianensis*. It differs from the modern genus *Dicerorhinus* in several cranial traits and is rather closer to the Middle Miocene Rhinocerotini from La Retama, suggesting the presence of an intracontinental dispersal during this time. Through comparison, we regard that the nasal notch is a good indication of the evolutionary level in Rhinocerotini, and the anterior position of the nasal notch represents the primitive stage. In this aspect, the anterior position of the modern *Dicerorhinus*, together with its overall similarity to *Lartetotherium cixianensis* as compared with other Rhinoicerotini from the Late Miocene to the modern world, suggests that this genus has been rather conservative during its evolutionary history, which is possibly related to the stable environment present in the tropical/subtropical forest in southeastern Asia, which brought a low level of selective pressure as food sources were abundant. Jiulongkou is the only Middle Miocene locality in China with Rhinocerotini. Together with its faunal composition, this implies a more humid and closed environment, in contrast to those from more the central and western parts of China at this time.

河北磁县九龙口中中新世动物群真犀的再研究

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摘要：现代犀牛都属于犀科中的真犀族，目前中国最早的真犀族动物化石记录是来自河北磁县九龙口中中新世的磁县"双角犀"，化石材料为幼年头骨和下颌。分析研究认为：这个物种与现生的双角犀*Dicerorhinus*的确存在相似之处，但也存在一些头骨结构上的差异，不应该被归入现生属。九龙口的真犀其实更加接欧洲中中新世的拉尔泰犀*Lartetotherium*，尤其是西班牙La Retama中中新世的材料，并应该归入该属。这一发现指示此时在欧亚大陆两端存在生物迁徙交流。九龙口动物群是中国中中新世目前唯一记录有真犀族动物的化石点，说明其环境相对湿润封闭，和当时中国更靠西北的化石点存在差异。研究发现鼻切迹位置是真犀族动物演化中具有较好演化水平指示意义的特征。现生苏门犀鼻切迹相对靠前以及其整体与磁县拉尔泰犀的相似性，指示这个属在与史蒂芬犀、披毛犀等更特化的双角犀分化后超过1000万年的演化历史中，只经历了比较小的形态学变化，这可能和南亚/东南亚地区环境相对稳定，选择压力较低有关。

关键词：九龙口，中中新世，磁县拉尔泰犀，真犀族

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